

Modeling expansion of individual leaves in the potato canopy

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Abstract

A model to simulate expansion of individual leaves in potato (*Solanum tuberosum* cv. Kennebec) was developed by modifying a growth simulation routine from the model POTATO. Data for model development and testing were obtained from three soil–plant–atmosphere-research (SPAR) chamber experiments. The first experiment (D1) used six SPAR chambers with treatments of 14/10, 17/12, 20/15, 23/18, 28/23, or 34/29 °C day/night temperatures (16 h thermoperiod) at an elevated atmospheric carbon dioxide concentration ($[CO_2]$) of $740 \mu\text{mol mol}^{-1}$. Experiment D2 used two SPAR chambers at 23/18 °C at $740 \mu\text{mol mol}^{-1}$ $[CO_2]$. Experiment D3 duplicated the temperature treatments of D1 but at ambient $[CO_2]$ ($370 \mu\text{mol mol}^{-1}$). Potato leaf area expansion was sensitive to air temperature and $[CO_2]$. Maximum individual leaf area values were highest at cooler temperatures and elevated $[CO_2]$. Growth duration, defined as the time interval between leaf appearance and when 99% of final area was attained, was negatively correlated with increasing temperature. Growth duration increased by about 4 days at 14/10 and 34/29 °C at ambient $[CO_2]$. Temperature response and leaf physiological aging functions were developed from D1 and used to modify the existing growth model. D2 and D3 data were used to evaluate the modified model simulations during conditions of non-limited and limited carbohydrate availability. By varying an input to the model that simulates the effect of plant carbohydrate status on leaf expansion, the model was shown to be capable of reproducing leaf growth curves within 8% of the measured final area. The modified leaf expansion model is suitable for integration with existing potato models that simulate canopy leaf appearance. The expansion model provides an approach for coupling plant assimilate, water, and nutrient status with canopy expansion and the new response functions in the model can potentially be modified for use in different crop models.

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1. Introduction

Appearance, expansion, and duration of individual leaves are critical determinants of potato canopy growth and development. Potato models typically simulate canopy development as an overall increase in leaf area index instead of focusing on individual leaves (e.g. IBSNAT, 1993; Kooman and Haverkort, 1995; Shay-

kewich et al., 1998). However, potato crop model predictions in response to environment, assimilate partitioning, and nitrogen can be improved by focusing at the individual leaf level (Vos, 1995). Little efforts have focused on modeling at the leaf level presumably due to lack of suitable modeling approaches and data sets. Several recent studies have been conducted to simulate individual leaf appearance rates in potato (e.g. Cao and Tibbitts, 1995; Fleisher et al., 2006). However, work is needed to develop a mechanistic approach to simulate the expansion of these leaves once they appear in the canopy.

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The expansion of the potato canopy for several days after emergence is highly correlated with air temperature (van Delden et al., 2000; Vos, 1995). Most potato models estimate leaf area expansion rate as an exponential function of cumulative thermal time. Once a pre-defined stage of potato development is reached, a linear relationship between leaf area growth and intercepted photosynthetically active radiation (PAR) is used to predict canopy expansion (e.g. IBSNAT, 1993; Kooman and Haverkort, 1995; Shaykewich et al., 1998). Conceptual carbohydrate pools for total canopy leaf and stem mass are computed by way of empirical partitioning coefficients. Leaf carbohydrate content is derived by using a fixed ratio between leaf area to dry mass, specific leaf area (SLA; $\text{cm}^2 \text{ leaf g}^{-1} \text{ dry mass}$). Thus, in order to move to an individual leaf basis, leaf expansion responses to temperature and plant assimilate supply need to be obtained.

Empirical growth curves have been used by researchers (e.g. Jefferies, 1993; Kirk and Marshall, 1992) to indicate the sigmoidal growth pattern of individual leaf area expansion versus time (Dale and Milthorpe, 1983). The CERES-Sorghum model (Ritchie et al., 1998) calculates potential leaf blade area expansion as a function of leaf tip position on the main stem and a cultivar specific maximum expansion rate using a Gompertz relationship (Thornley and Johnson, 1990) similar to Eq. (1). The estimate for leaf area is modified by empirical factors for water and nitrogen deficiencies in the plant:

$$A = A_0 \exp \left[\ln \left(\frac{A_f}{A_0} \right) (1 - \exp(-D \cdot \text{DAA})) \right] \quad (1)$$

where A_0 is the initial leaf area at appearance (0.05 cm^2), A_f the final leaf area achieved (cm^2), A the leaf area (cm^2), D the decay in specific leaf expansion rate (day^{-1}), and DAA is the days after appearance of leaf (day).

POTATO (Ng and Loomis, 1984) is one of the few explanatory type potato models that simulates individual organ (i.e. leaves, stems, roots, stolons, and tubers) growth by distinguishing between organ relative growth rate and the duration of growth. In their model, organ growth rate proceeds at a maximum relative rate, R_{\max} (Eq. (2)). R_{\max} is modified by the fraction or percentage of the cells in the organ capable of additional growth or expansion, $f(\text{age})$. This fraction is a function of the physiological age of the organ. The influence of air temperature on cell expansion rate, $f(T)$, modifies the organ growth at each time-step. Eq. (2) is modified by empirical factors, ranging from 0 to 1, that simulate the

influence of limiting plant water, nutrient and assimilate status:

$$R = WR_{\max} f(\text{age}) f(T) \quad (2)$$

where R is the organ growth rate (g day^{-1}), R_{\max} the maximum relative rate of organ growth ($\text{g g}^{-1} \text{ day}^{-1}$), W the organ weight (g), $f(\text{age})$ the physiological age dependent expansion rate (g g^{-1}) and $f(T)$ is the air temperature affect on cell division and expansion (unit less, 0–1).

Ng and Loomis (1984) estimated leaf area expansion by multiplying leaf growth rate R (g day^{-1}) by SLA. Empirical factors for light intensity and leaf age were used to modify the relationship between leaf area and dry mass. Due to lack of data on individual leaf expansion, response functions for $f(T)$ and physiological leaf age were derived from potato internode elongation studies and temperature responses for leaf appearance rates (Ng and Loomis, 1984). A linear relationship was used to describe the relationship between leaf physiological age and the fraction of the leaf still capable of growth ($f(\text{age})$). R_{\max} was also assumed to be the same for tubers, stems, leaves, and stolons.

In validating the model, Ng and Loomis (1984) cited these temperature-based functions as a primary reason for discrepancies between simulated and predicted leaf area. In addition, leaf growth may be more appropriately modeled on a leaf area expansion basis. Tardieu et al. (1999) and Bertin and Gary (1998) concluded that increases in individual leaf expansion were not causally connected with increases in dry mass within certain limits of whole plant assimilate supply. However, young leaves, which are incapable of producing enough photosynthate to support their own growth demand, must import carbon from other sources in the plant. These results indicate that leaf expansion in younger leaves should be modeled as an incremental increase in area rather than accumulation of carbohydrate, particularly when the assimilate supply in the plant is limiting.

Information on potato leaf expansion under non-limiting growth conditions, such as elevated atmospheric carbon dioxide concentration [CO_2], is also needed to improve individual leaf growth simulations. Potatoes generally show a large positive response with [CO_2] enrichment with increased yield and total mass (Collins, 1976; Wheeler et al., 1991; Yandell et al., 1988). Potato leaf sizes and total leaf mass in the canopy were shown to also exhibit a positive response (Wheeler et al., 1991) but information on individual leaf expansion is not available.

Our objectives were to (1) obtain experimental data on the time course of potato main stem leaf expansion at

Table 1

Average 24-h air (T_{air}) and canopy temperatures (T_{can}) ($^{\circ}\text{C}$) and standard deviations (S.D.) during the measurement period for experiments D1, D2, and D3

Treatment ($^{\circ}\text{C}$)	Temperature											
	D1				D2				D3			
	T_{air}	S.D.	T_{can}	S.D.	T_{air}	S.D.	T_{can}	S.D.	T_{air}	S.D.	T_{can}	S.D.
14/10	12.9	0.37	14.1	0.61	–	–	–	–	12.8	0.39	14	1.46
17/12	15.7	0.20	16.9	0.5	–	–	–	–	15.9	1.47	17.1	1.1
20/15	19.4	0.07	21.3	0.65	–	–	–	–	19.3	0.19	20.9	0.8
23/18	22.1	0.16	21.6	0.49	21.4	0.05	22.7	0.74	22.1	0.11	21.4	1
28/23	26.8	0.14	25.7	1.11	–	–	–	–	26.7	0.18	26.6	0.63
34/29	31.9	0.23	32.9	0.54	–	–	–	–	32.1	0.34	33.3	0.62

different air temperatures under limiting (ambient [CO_2]) and non-limiting (elevated [CO_2]) growth conditions, (2) develop new temperature response and aging functions for Eq. (2), (3) modify the equation to a form suitable for simulating potential leaf area expansion, and (4) evaluate the capability of using the model to simulate potato leaf expansion under carbon limiting conditions. Methods of integrating this new approach for simulating individual leaf expansion as part of a full potato canopy model area are discussed.

2. Materials and methods

2.1. Experiments

Three experiments, two at elevated [CO_2] (D1 and D2), and a third at ambient [CO_2] (D3) were conducted at USDA-ARS facilities located in Beltsville, MD in the summers of 2004 and 2005.¹ Certified potato (*Solanum tuberosum* cv. Kennebec) seed tubers (54.9 ± 10.04 g mean fresh weight) were planted in 15 l pots at a depth of 5 cm. Pots were filled with a 50/50 peat-vermiculite potting medium in D1 and D3 and a 3:1 (by volume) sand-vermiculite medium in D2.

In D1 and D3, plants were kept in reach-in growth chambers (Environmental Growth Chambers, Chagrin Falls, OH, USA) maintained at 20°C with a 16 h photoperiod and $550 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) ($6.61 \text{ MJ PAR m}^{-2} \text{dat}^{-1}$) until 12 DAE (days after emergence) in D1 and 5 DAE in D3. Plants were selected for uniformity, thinned to a single main stem per pot, and relocated to one of six outdoor Soil–Plant–Atmosphere–Research (SPAR)

chambers (12 plants m^{-2}). In D2, pots were placed in the SPAR chambers prior to emergence.

SPAR chambers were constructed with clear acrylic and transparent to natural sunlight. Air was constantly re-circulated in a closed loop at 3 m s^{-1} . A dedicated Sun SPARC 5 work station (Sun Microsystems, Inc., Mountainview, CA, USA) logged environmental data (air and soil temperatures, canopy temperature, relative humidity, [CO_2], and solar radiation) every 300 s. Addition detail on SPAR chamber operation and design may be found in Reddy et al. (2001).

In D1 and D3, each SPAR chamber was set to one of six different day/night temperature regimes, 14/10, 17/12, 20/15, 23/18, 28/23, and 34/29 $^{\circ}\text{C}$ with a 16 h day/night thermo-period. In D2, all SPAR chambers were maintained at $23/18^{\circ}\text{C}$ but received different amounts of nitrogen fertilizer. The two chambers with the highest values of nitrogen in the fertilizer (11 and 14 mmol N l^{-1}) were used in this manuscript. Average 24-h air and canopy temperatures throughout the measurement period for each treatment are reported in Table 1. Average, maximum, and minimum photosynthetic irradiance was 7.13 , 10.05 , and $1.78 \text{ MJ PAR m}^{-2} \text{day}^{-1}$ in D1, 9.1 , 12.0 , and $1.71 \text{ MJ PAR m}^{-2} \text{day}^{-1}$ in D2, and 7.76 , 12.04 , and $1.6 \text{ MJ PAR m}^{-2} \text{day}^{-1}$ in D3.

Relative humidity was maintained at 75% and the photoperiod was approximately 14.3 h in all experiments. [CO_2] was controlled so that a minimum of $740 \mu\text{mol mol}^{-1}$ was maintained at all times during the day in D1, $370 \mu\text{mol mol}^{-1}$ in D2, and $696 \mu\text{mol mol}^{-1}$ in D3. Nighttime [CO_2] was uncontrolled and ranged between 554 and $1000 \mu\text{mol mol}^{-1}$ for all experiments. Fiberglass shading material was erected around each chamber at DAE 14 and raised twice per week to match canopy height so as to minimize border effects. In D1 and D3, plants were irrigated once per day with tap water (2 l per pot). Each pot received 500 ml of nutrient solution described in Robinson (1984) twice per week

¹ Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA and does not imply the exclusion of other available products.

prior to 30 DAE and 1000 ml after 30 DAE. In D2, pots were watered every day with 300 ml of nutrient solution. Once per week, all pots were watered to capacity with tap water.

2.2. Measurements of leaf area

The potato leaf is a compound leaf consisting of primary and secondary leaflets (Kirk and Marshall, 1992). Leaf growth following unfolding (i.e., leaf appearance) from the subtending branch is generally responsible for over 95% of total dry weight and more than 99% of total leaf area at final expansion (Dale and Mithorpe, 1983). Thus, leaf area measurements obtained from the time period between visual appearance of the unfolded leaf until it achieves full expansion are suitable for modeling individual leaf expansion rates.

A minimum leaf length (0.5 cm) of the unfolded leaf from the apical bud is typically used to indicate date of appearance of the potato leaf (Cao and Tibbitts, 1995; Kirk and Marshall, 1992; Vos and Biemond, 1992). Non-destructive measurements of individual leaf terminal length (L ; cm), defined as the distance from the stem to the tip of the terminal leaflet, and width of the compound leaf (W ; cm) were obtained starting at the day of leaf appearance. In D1 and D3, measurements were recorded for main stem leaves between nodes 5 and 14 (as counted from the soil surface) on 5 plants per chamber twice per week. In D2, measurements were made on main stem nodes 9 and 12. Leaf measurements were stopped on a

particular leaf when no further increase in L and W on three successive dates was observed. Leaf length and width data were converted to leaf area (A ; cm²) using Eq. (3). Eq. (3) was obtained from L , W , and leaf area data (measured with a Li-Cor 3100 area meter (Li-Cor, Lincoln, Nebraska, USA)) from leaves randomly harvested from plants not used in the measurements in each treatment following Vos and van der Putten (1998) and Benoit et al. (1986):

$$A = 0.872LW \quad (r^3 = 0.93; \text{ S.E.} = 0.003; n = 25) \quad (3)$$

where L is the terminal leaflet length (cm) and W is the width of compound leaf (cm).

2.3. Data analysis

SAS software (The SAS system for Windows, 8.02, SAS Institute, Inc., Cary, NC, USA) was used to perform all statistical procedures using REG and NLIN procedures for linear and nonlinear regression analysis. Leaves from main stem nodes 7–12 within the same treatment were pooled together for the analysis in D1 and D3 and 9 and 12 in D2. In D1 and D3, higher leaves on the main stem were dropped from analysis because their expansion was presumed to be limited due to competition for assimilate from other parts of the plant. This was particularly true in the warmer temperature treatments where significant lateral branching and secondary leaf growth had occurred prior to appearance of higher nodes

Table 2

Gompertz parameters (defined in Eq. (1)), standard errors (S.E.), sample size (n), and r^2 values for pooled leaf area measurements in experiments D1, D2, and D3

Treatment ^a	A_f (cm ²)	S.E.	D (day ⁻¹)	S.E.	n^b	r^2	G_{dur}^c (day)	S.E. ^c
D1-34/29	52.0	2.13	0.4170	0.0523	53	0.947	15.7	1.97
D1-28/23	181.9	5.85	0.3880	0.0377	86	0.944	17.3	1.68
D1-23/18	247.6	7.48	0.2840	0.0236	82	0.987	23.8	1.97
D1-20/15	279.9	8.58	0.2796	0.0226	72	0.961	24.2	1.95
D1-17/12	300.7	8.36	0.2002	0.0116	83	0.94	33.8	1.96
D1-14/10	327.3	5.58	0.1740	0.0052	63	0.945	39.0	1.16
D2-23/18 a	235.2	24.8	0.2868	0.034	51	0.82	23.5	2.78
D2-23/18 b	253.9	16.57	0.3286	0.03	55	0.88	20.5	1.87
D3-34/29	51.9	2.56	0.2909	0.0468	44	0.935	22.5	3.62
D3-28/23	162.0	4.86	0.3282	0.0276	78	0.946	20.4	1.71
D3-23/18	157.1	7.52	0.3128	0.0458	78	0.882	21.4	3.13
D3-20/15	287.1	7.85	0.2502	0.0201	77	0.958	27.0	2.17
D3-17/12	236.0	8.52	0.1600	0.0103	84	0.944	42.1	2.71
D3-14/10	214.8	9.15	0.0124	0.0103	83	0.924	47.2	3.42

^a Two chambers (a and b) were used in D2 at the same growth temperature.

^b Total number of leaves measured from all plants in each treatment. Each leaf was measured two times per week following leaf appearance.

^c Growth duration (G_{dur}) was estimated as the number of days after leaf appearance needed to achieve 99% A_f . Uncertainty estimates were obtained from the standard errors of A_f and D following Moffat (1985).

on the main stem (data not shown). Nodes 5 and 6 were not included because they had initiated prior to transferring the plants into the SPAR chambers.

3. Results

3.1. Leaf expansion data

The Gompertz growth equation (Eq. (1)) was fit (correlation coefficients 0.82 or higher) to pooled main stem leaf area data versus the corresponding number of days after leaf appearance (DAA) from each experiment (Table 2, Fig. 1). Estimated values for maximum leaf area, A_f (cm²), and the time to achieve 99% of A_f , G_{dur} (days), or growth duration, were obtained for each temperature treatment (Table 2, Fig. 2).

Relative responses of A_f were similar between ambient and elevated [CO₂] datasets and followed a quadratic response with temperature (Fig. 2A). Comparison of the regression coefficients (not shown) for D1 and D3 in Fig. 2A indicated that the quadratic response was the same but linear terms were significant different. This implies that both treatments exhibit a similar response to the extreme, but not middle temperature treatments. A_f values were larger in D1 and D2 than in D3 over the range of temperatures studied except at 20 °C (the 23/18 °C treatment) (Fig. 2A, Table 2).

G_{dur} also exhibited a nonlinear relationship with increasing temperature, with values decreasing as temperature increased (Table 2, Fig. 2B). G_{dur} values were similar for all experiments at a given temperature. A comparison of regression coefficients (not shown)

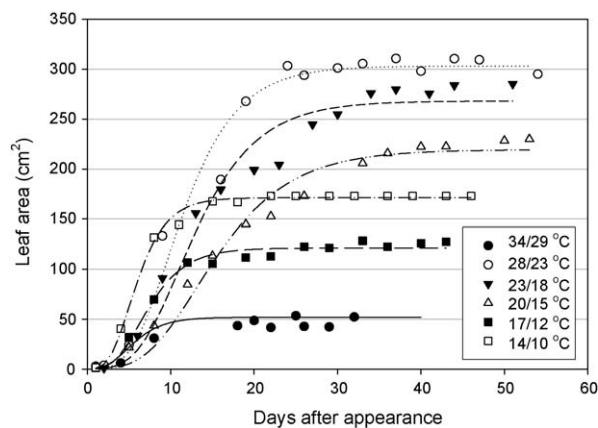


Fig. 1. Measured (symbols) and simulated (lines) individual leaf area versus days after appearance for experiment D1. Measured data are the average main stem leaf area from five plants per treatment (standard deviations not shown to improve clarity). Simulated lines were obtained using the Gompertz equation (Eq. (1)) with parameters and correlation coefficients in Table 2.

indicated non-common intercepts, indicating that D3 leaves took slightly longer to reach their maximum expansion than D1. The differences in G_{dur} between D1 and D3 primarily occur at the extremes of the temperature range at the 34/29 and 14/10 °C treatments (Fig. 2B). A_f and G_{dur} values for D2 chambers were similar to the 23/18 °C treatment in D1.

3.2. Model development

Eq. (2) was modified to express the potential daily rate of leaf expansion, L , on an area basis (Eq. (4)). L can proceed at a maximum potential rate, L_{max} , modified by the physiological age of the leaf ($f(\text{age})$), air temperature ($f(T)$), and limiting effects of plant assimilate supply on expansion ($f(C)$). D1 data was used to develop new response functions for leaf area expansion and D2 and D3 were used to evaluate the simulated results. It was assumed that leaf expansion was not limited by assimilate supply, water or nutritional stresses in D1:

$$L = AL_{max} f(\text{age}) f(T) f(C) \quad (4)$$

where L is the rate of leaf area expansion (cm² day⁻¹), L_{max} the maximum relative rate of area expansion (cm² cm⁻² day⁻¹), A the leaf area (cm²), $f(\text{age})$ the

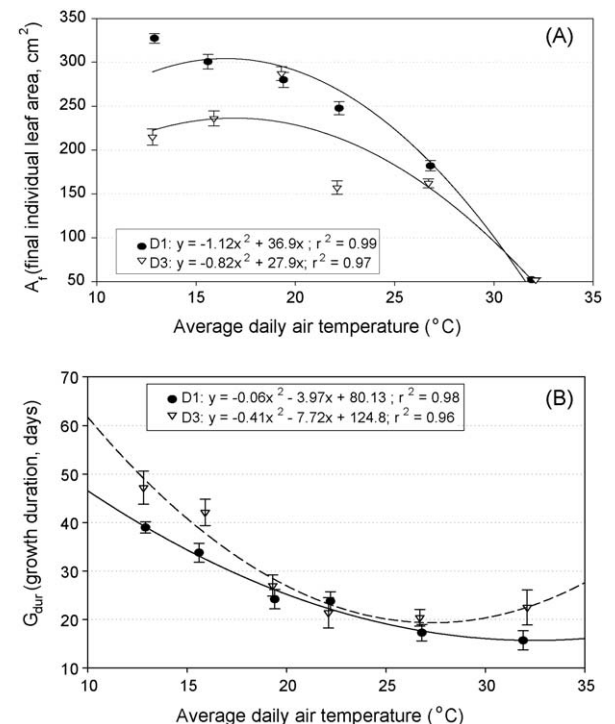


Fig. 2. Final leaf area, A_f (A) and growth duration, G_{dur} (B) with standard errors (Table 2) vs. average daily air temperature for experiment D1 (elevated [CO₂]) and D3 (ambient [CO₂]).

physiological age dependent expansion rate ($\text{cm}^2 \text{cm}^{-2}$), $f(T)$ the air temperature affect on cell division and expansion (unit less, 0–1), and $f(C)$ is the affect of assimilate supply on potential leaf expansion (unit less, 0–1).

The highest L_{\max} value, $9.7 \text{ cm}^2 \text{cm}^{-2} \text{day}^{-1}$, was observed at the $28/23^\circ \text{C}$ treatment of D1 (not shown); thus, a value of $10 \text{ cm}^2 \text{cm}^{-2} \text{day}^{-1}$ was assumed to represent the genetic maximum potential expansion rate. Physiological leaf age and the relative rate of leaf cells to continue to divide and expand are expressed by the $f(\text{age})$ function. Physiological leaf age is dependent on air temperature as in Ng and Loomis (1984). From G_{dur} values in Table 2, it was assumed that 15 physiological days (15 days-p) were required for leaves to reach their full size. Thus, leaf area expansion ceases at 15 days-p, although the leaf can continue to increase in mass via photosynthesis or import of carbohydrate from other sources in the plant once this threshold is exceeded. Dependency of physiological leaf age on temperature was obtained by dividing 15 by G_{dur} at each temperature treatment. Fig. 3 shows this aging temperature response (days-p $^\circ \text{C}^{-1}$) from each treatment. At 4°C , it is assumed that leaf physiological aging (and development) in potato ceases (Firman et al., 1991; Kirk et al., 1985) (Eq. (5)):

$$P = 0.029T + 0.031 \quad (5)$$

where P is the increase in leaf physiological age at current time increment (days-p) and T is the average air temperature during time increment ($^\circ \text{C}$).

The relative leaf expansion rate (L_R , Eq. (6)) exponentially decays as leaf physiological age increases. L_R were normalized by dividing Eq. (6) with

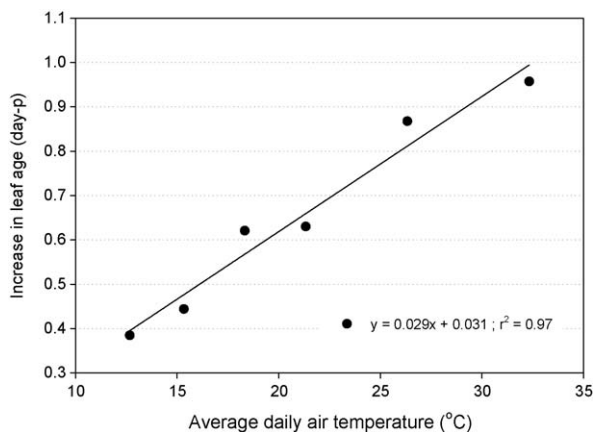


Fig. 3. Leaf physiological aging (days-p) as a function of average daily (24-h) air temperature. Leaf expansion ceases when the cumulative number of days-p exceeds 15.

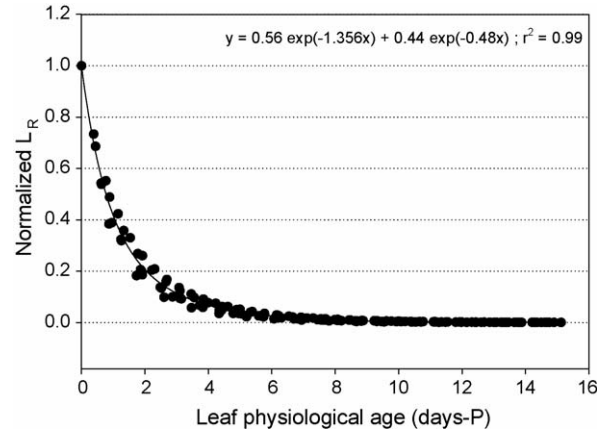


Fig. 4. Normalized relative leaf expansion rate, L_R , vs. leaf physiological age for all temperature treatments in D1. Parameter for the double exponential decay equation (solid line) fit through the data were $a = 0.5586$, $b = 1.3563$, $c = 0.4431$, and $d = 0.4813$ ($n = 157$).

the maximum relative rate of expansion observed for each temperature treatment. Normalized L_R were plotted against physiological leaf age (Fig. 4). A double exponential decay equation (Eq. (7)) was fit to the data. Differences the maximum relative rate of expansion between treatments were used to develop the $f(T)$ response (Fig. 5). A four-parameter log normal curve was fit to the data to adequately describe the response with temperature (Eq. (8)):

$$L_{Ri} = \frac{1}{A_i} \left(\frac{A_i - A_{i-1}}{1} \right) \quad (6)$$

where L_{Ri} is the relative rate of expansion at time i ($\text{cm}^2 \text{cm}^{-2} \text{day}^{-1}$), A_i the leaf area at time i (cm^2) and 1

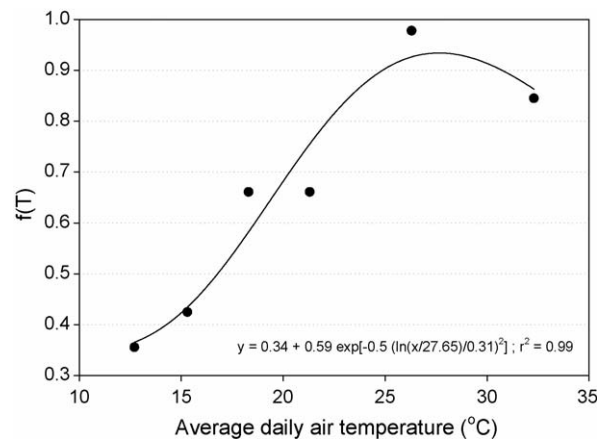


Fig. 5. Influence of temperature on cell division and expansion, $f(T)$, vs. average daily air temperature. Parameters for the log normal equation (solid line) fit through the data were $a = 0.34$, $b = 0.5927$, $c = 27.65$, and $d = 0.3075$ ($r^2 = 0.996$).

is the time step (1 day):

$$L_R = a e^{-bt} + c e^{-dt} \quad (7)$$

where a , b , c and d are the empirical coefficients defined in Fig. 4 and t is the physiological age (days-p):

$$f(T) = a + b \exp \left[-0.5 \left(\frac{\ln(T/c)}{d} \right)^2 \right] \quad (8)$$

where a , b , c , and d are the empirical coefficients defined in Fig. 5 and T is the air temperature ($^{\circ}\text{C}$).

In Eq. (4), $f(C)$ ranges from 0 to 1 depending on whether the supply of carbohydrate in the plant (and fixed via photosynthesis by the leaf itself) is sufficient to support area expansion of the individual leaf. It is assumed that $f(C) = 1$ in the development of the leaf expansion model from dataset D1 with elevated $[\text{CO}_2]$. However, by setting $f(C)$ to values less than 1, other less optimal situations can be simulated.

3.3. Simulation results

The leaf expansion model was tested using a daily (24-h) time-step. Values for leaf physiological age (Eq. (5)), the effect of leaf age on normalized relative leaf expansion rate (Eq. (7)), and $f(T)$ (Eq. (8)) are estimated using the average air temperature during each time increment. New leaf area growth (L) is computed as in Eq. (4), assuming an initial leaf area of 0.05 cm^2 at 0 days after appearance. Root mean square difference (RMSD) (Eq. (9)) and the percent deviation from final leaf area were used to evaluate the model fit to experimental data. Goodness of fit information for the

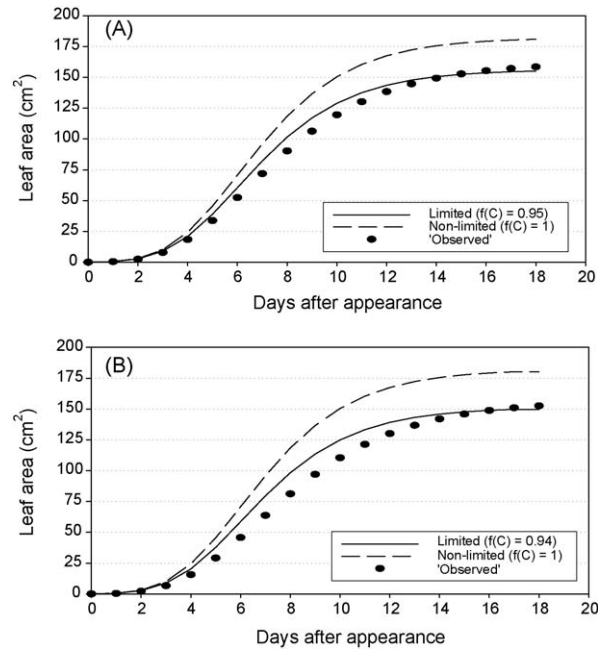


Fig. 6. Leaf area vs. days after appearance for 23/18 $^{\circ}\text{C}$ (A) and 28/23 $^{\circ}\text{C}$ (B) treatments of experiment D3. ‘Observed’ – leaf area predicted using Gompertz equation (Table 2); limited or non-limited – expansion is limited or non-limited by carbohydrate during first 4 days of expansion as simulated with $f(C)$ values (Table 3).

leaf expansion model versus datasets D1, D2, and D3 are summarized in Table 3 for all simulations:

$$\text{RMSD} = \sqrt{\frac{\sum_{i=1}^n (\text{observed}_i - \text{predicted}_i)^2}{n}} \quad (9)$$

Table 3

Comparison of leaf expansion model predictions with experimental data for two scenarios: (1) non-limiting assimilate supply ($f(C) = 1$) and (2) limited assimilate supply ($f(C) \leq 1$)

Treatment	Scenario (1) (non-limiting)			Scenario (2) (limiting)		
	RMSD (cm^2)	% deviation from A_f	$f(C)$ value	RMSD (cm^2)	% deviation from A_f	$f(C)$ value
D1-14/10	6.195	1.07	1	–	–	–
D1-17/12	6.855	–1.27	1	–	–	–
D1-20/15	2.857	–0.917	1	–	–	–
D1-23/18	3.776	–1.979	1	–	–	–
D1-28/23	5.302	–0.209	1	–	–	–
D1-34/29	0.593	–0.123	1	–	–	–
D2-23/18 a	13.78	7.52	1	–	–	–
D2-23/18 b	16.84	–0.45	1	–	–	–
D3-14/10	99.61	–54.18	1	19.62	2.52	0.84
D3-17/12	75.11	–32.54	1	22.07	3.69	0.89
D3-20/15	11.87	0.74	1	11.87	0.74	1
D3-23/18	22.60	–14.13	1	6.02	2.14	0.95
D3-28/23	29.29	–18.51	1	9.39	1.89	0.94
D3-34/29	8.96	–6.14	1	7.24	0.98	0.98

In simulating D2 data, leaf expansion was assumed to be non-limited as the $[\text{CO}_2]$ was approximately twice that of ambient; therefore, $f(C)$ was set equal to one. Two separate simulations were run against the data in D3. In the first case, leaf expansion in D3 is assumed to be non-assimilate limited and $f(C)$ is therefore equal to 1. In the second case, D3 is assimilate limited, and $f(C)$ varies as described below. RMSD values were less than 7 cm^2 and the deviation from final leaf area was within $\pm 2\%$ for all treatments in D1. In D2, RMSD values were 13.8 and 16.8 cm^2 for each chamber and final leaf area was within 8% of predicted. Simulated leaf expansion values with respect to D3 data were over-predicted by a minimum of 6% and a maximum of 54% for all treatments except 20/15 °C.

In the second simulation for D3, it was assumed that carbohydrate supply was a limiting factor on leaf expansion for the first 4 days following leaf appearance. Values for $f(C)$ were obtained by minimizing the sum of percent deviation from observed A_f and RMSD values. Percent deviations are within 4% of the final area values in this case (Table 3). Fig. 6 illustrates the change in leaf expansion when simulating the limiting effects of assimilate supply at 23/18 °C (A) at 28/23 °C (B) in D3.

4. Discussion

4.1. Data and modeling approach

Published data on the response of individual leaf area expansion with $[\text{CO}_2]$ is scarce. However, Wheeler et al. (1991) and Collins (1976) observed increases in total canopy leaf area with $[\text{CO}_2]$ that were consistent with our observations of total leaf area at harvests of D1 and D3 (data not shown). The increase in individual leaf final area with $[\text{CO}_2]$ over most of the temperature range studied is consistent with these observations (Fig. 2B). The temperature response at ambient $[\text{CO}_2]$ (Fig. 2A, Table 2) were similar to those reported by Kirk and Marshall (1992) where maximum individual leaf lengths were observed at 16 °C and then declined at cooler temperatures. The similar A_f values in D1 and D3 at 20 °C (23/18 °C treatment) (Fig. 2A) indicate that growth expansion for main stem leaves was not limited by carbohydrate supply at this temperature in either experiment. At this temperature, less leaves formed in the canopy than at warmer treatments in both D1 and D3 (data not shown). Higher canopy gas exchange values were measured at this temperature compared with the cooler treatments in D1 and D3 (data not shown),

supporting the conclusion that leaf expansion was not limited by assimilate supply.

The nonlinear relationship between G_{dur} and temperature was also noted by Kirk and Marshall (1992). G_{dur} values were similar for all three experiments (Fig. 2B); however, a slightly longer period of time was required for leaves to reach their final size in D3 at the 14/10 and 34/29 °C treatments. Firman et al. (1995), Jefferies (1993), Kirk (1986), and Vos and Biemond (1992) indicated that the duration of expansion of leaves at higher positions in the potato canopy could be influenced by nitrogen supply. However, the leaf expansion model presented in this paper assumed G_{dur} was solely influenced by temperature; thus, the leaf expansion model can be improved by incorporating additional factors that affect leaf physiological aging or expansion rate.

A major assumption in the leaf expansion model was that the average main stem A_f values in D1 and D2 were not limited by carbohydrate, water, and nitrogen supply. At these conditions, organ growth rates should proceed at their maximum potential (Reddy, 1994). Since A_f and G_{dur} were similar for D1 and D2 (Table 2) and average photosynthetic irradiance was comparable (7.1 and $9.1 \text{ MJ PAR m}^{-2} \text{ day}^{-1}$ in D1 and D2 respectively), this assumption was valid. Photosynthetic irradiance for D3 was also similar to D1 ($7.7 \text{ MJ PAR m}^{-2} \text{ day}^{-1}$) but atmospheric $[\text{CO}_2]$ was half of the value, indicating that the smaller leaf areas in D3 were likely the result of reduced plant assimilate supply. At harvest, plants within a given temperature treatment at elevated $[\text{CO}_2]$ (D1 and D2) also had significantly larger biomass than at ambient (D3) (data not shown). Thus, one would expect the model to over-estimate leaf expansion in potatoes grown under limiting carbohydrate conditions unless provisions were made to account for plant carbon status in the model.

The use of $f(C)$ in the model to simulate this limiting effect of assimilate supply in young leaves is justified. Leaf expansion is particularly sensitive to plant assimilate status when leaves are newly emerged. Dale and Milthorpe (1983) reported that new leaves import the majority of carbohydrate from other sources in the plant to support expansion growth. This dependency on assimilate supply declines as the leaf reaches 20–30% of its final area, at which point the leaf is capable of synthesizing most of its own photosynthate. Tardieu et al. (1999) found that the rate of expansion of young, newly unfolded leaves was strongly dependent on plant carbohydrate supply, while the growth rate of older, more mature leaves was not affected when portions of the plant were shaded. In their study, leaves that were

newly emerged at the time of the shading treatment was applied had smaller A_f values (G_{dur} was unaffected). Also, when shading was removed, the relative rate of leaf area expansion in the young leaves immediately returned to match that of the control; however, actual leaf area was permanently reduced. Thus, leaf area and relative expansion rate, but not growth duration, of young leaves is highly dependent on plant carbohydrate supply during initial expansion stages following leaf appearance, supporting the scenario 2 analysis for D3 in Table 3.

4.2. Integration with explanatory crop models

The leaf expansion model, when coupled with routines for leaf appearance rate (e.g. Fleisher et al., 2006) and leaf duration, is suitable for improving the canopy growth and development component in explanatory potato models. In SIMPOTATO (Hodges, 1992) the amount of daily carbohydrate fixed via photosynthesis by the plant is a function of light interception and canopy leaf area index. This carbohydrate pool is partitioned among leaves, roots, stems, and tubers based on partitioning coefficients that vary with environment and plant developmental stage. Under most production conditions, the expansion rate of all leaves in the canopy is limited by the quantity of carbohydrate available. Specific leaf area (the ratio of leaf area per gram of leaf dry mass) is used to relate leaf area expansion with carbohydrate gain. If the individual leaf expansion model developed in this manuscript is used in a modified version of SIMPOTATO, the $f(C)$ component in Eq. (4) could be adjusted in newly emerged leaves based on leaf age and the difference between the amount of carbohydrate needed to satisfy potential expansion demand and the actual amount of carbohydrate available. Initial simulations using this procedure resulted in prediction errors between 5 and 15% of maximum leaf area from D3 data, an improvement over the un-modified model's predictions (not shown). By varying the $f(C)$ value for newly emerged leaves, it is possible to simulate differences in A_f that have been observed for leaves at higher positions on the main stem and other lateral branches (Firman et al., 1995; Kirk and Marshall, 1992; Vos and Biemond, 1992).

The modified leaf expansion model and new temperature response and aging functions developed in this paper present a more mechanistic platform than previous models in which to incorporate nitrogen and water responses into a comprehensive leaf expansion approach. The model can potentially be used for

simulation at hourly or smaller time-steps so that significant short-term fluctuations in assimilate, nutrient or water status could be incorporated. By coupling the leaf expansion model with similar routines for leaf appearance, duration, and potato growth and phenology, the approach will improve accuracy and robustness of potato crop models to reproduce and emulate potato responses to fluctuating growth conditions during production. The response functions in the modified leaf expansion model can also be adapted to simulate leaf expansion in other crop models.

5. Conclusions

A model for simulation of individual leaf expansion in potato was developed by modifying an existing potato organ growth model. New response functions for leaf physiological aging, the fraction of leaf capable of expanding at the current time increment, and the influence of air temperature on leaf expansion were obtained. These functions were derived from measurements of leaf area in potato plants grown in growth chambers at 14/10, 17/12, 20/15, 23/18, 28/23 and 34/29 °C day/night temperatures with a 16 h thermoperiod at 740 $\mu\text{mol mol}^{-1}$ [CO_2]. Data from two additional experiments conducted at ambient and elevated [CO_2] were used to evaluate the model. The model was accurate (within 8% of predicted values) in simulating non-carbon limited leaf expansion. By varying a factor that simulates the influence of limiting plant assimilate supply on leaf expansion, the model was shown to accurately reproduce leaf area (within 4% of predicted values) and growth duration at varying growth temperatures. The leaf expansion model is intended to be integrated with existing potato crop models in order to improve potato responses to varying growth conditions during production. Response functions developed for the leaf expansion model can also be adapted for other crops.

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